

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

1.

The Significance of Differential Locomotor Activity as an Index to the Mass Physiology of Fishes.

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(Text-figures 1-8).

INTRODUCTION.

The existence of a measurable differential in the locomotor behavior of fishes under various conditions of companionship has been established by Schuett (1934) and confirmed by Breder and Nigrelli (1935b) and Escobar, Minahan and Shaw (1936). Each report mentions the use of similar physical equipment but somewhat different handling of the data. All three are almost purely descriptive with little attempt to interpret the possible significance of the data obtained or to explain the mechanism responsible for the observed differences in behavior.

It is the purpose of the present communication, therefore, to interpret the findings of the various investigators and to correlate these results, so far as possible, with other known data on the social attitudes of fishes. To this end a considerable amount of experimental work is reported, some of which was briefly referred to by Breder and Nigrelli (1935b). It was early found that before the observable results could be satisfactorily interpreted it was necessary to consider in some detail the various items of both the internal and external environment. Supplementary experiments, that may seemingly have little bearing on the problem of social attitude or mass physiology, were found necessary.

Briefly stated, the method of investigation, which was devised by Dr. Paul Escobar and associates, consists of observing the successive positions of a fish in each of the three dimensions through a system of coordinates ruled on the glass walls of an aquarium. From such observations the distance traveled, the configuration of paths and their relation to the three spatial axes may be calculated. That these differ for any one specimen with companions and when alone has already been established in the three reports mentioned. Before going into a full discussion of these data and presenting more details of related matters, a brief consideration of the factors involved may best be presented.

FACTORS INVOLVED.

Of the numerous factors concerned, many are self evident, some are not, and a few have not been previously discussed in this connection. It does not follow, furthermore, that this list is exhaustive, but is intended to indicate only those factors that must be considered for any adequate understanding of social phenomena in fishes.

EXTERNAL FACTORS.

All the factors in the external environment may be considered under this head and so include all influences extrinsic to the subject itself.

Space. The available space places strictures on the movements of the included organisms. For example, any calculations based on physical formulae that assume an infinite medium are accordingly modified by the limits of the container.

The shape of the space as well as the volume is distinctly important. This has been discussed in considerable detail by Escobar, Minahan and Shaw (1936). Thus, its relative extent in reference to the vertical and horizontal axes is an important differential. This latter element is apparently due extrinsically entirely to the unidirectional nature of the gravitational influence, illumination, etc.

Radiant energy. The impact of radiant energy is of extreme importance since, for example, the presence of visible radiation is essential to vision, the eyes being important receptors in the aggregating behavior of fishes. Other wave lengths have not been studied in detail but Beebe (1935) showed that a beam of ultra-violet would cause certain fishes to aggregate in a closely compacted mass within its radius.

Temperature. The effects of thermal differences and thresholds are obviously of considerable importance to the differential behavior of fishes. Schooling in some cases is clearly temperature controlled; Townsend (1916) and Breder and Nigrelli (1934, 1935a). In these cases the lowering of temperature induces the fishes to aggregate.

Chemical conditions. Many substances dissolved in the water have a clear effect on the "social" attitude of fishes, including the amount of CO₂ and O₂ present; Allee (1931), Allee and Bowen (1932), Breder (1934), Breder and Nigrelli (1934, 1935a). Eddy (1925) maintained that certain stimulants caused aggregation and certain depressants caused dispersal.

Objects. What, for want of better term, may be considered as objects may include both those that are inert and those that are active. Rocks, plants, etc., serve in part to act as physical boundaries to the subjects but more especially as boundaries to their vision which, as will develop, are of considerable importance in the behavior pattern. Food items present a vigorous stimulation to hungry subjects.

The companions may be here classified as homotypic and heterotypic, following the usage of Escobar, Minahan and Shaw (1936). These may be attractive or repellant according to the particular physiological state of the subject at the time.

INTERNAL FACTORS.

Under this head may be considered all the effects of the internal environment. These then include the physical, chemical, and psychological make-up of the organism and cover all its inherent tendencies and characteristics.

The Receptors. Since all knowledge of the external world comes by way of the sensory receptors, considered in the broadest sense, they in their entirety may be taken as a starting point. It so happens that in all fishes

which have been used in experiments involving their attitude to their fellows, vision alone has been shown to be significant; Newman (1876) *Clupea harengus* Linnaeus; Parr (1927) *Pneumatophorus grex* (Mitchill); Spooner (1931) *Morone labrax* Linnaeus; Breder (1929) *Jenkinsia stolifera* (Jordan and Gilbert); Bowen (1931, 1932) *Ameiurus melas* (Rafinesque); Breder and Nigrelli (1934, 1935a) *Lepomis auritus* (Linnaeus). This has been in part demonstrated by the breaking up of schools on dark nights or by covering the eyes of individuals with vaseline and lamp black. While it has not been previously noted, the same holds for *Carassius auratus* (Linnaeus), the species on which Schuett (1934), Breder and Nigrelli (1935b) and Escobar, Minahan and Shaw (1936) chiefly worked. Consequently there is no need under the present limits of data to speculate on the possible significance of the other senses so far as response of fish to fish is concerned. However, the presence of chemically detectable food, mechanical jarring of the aquarium, etc., rapidly change the pattern of behavior and for the purpose of the present experimental studies have been rigorously guarded against.

The Effectors. After stimulæ are passed from the receptors and modified by the neuro-endocrine mechanism, the past conditioning of the fish, the particular drives that it labors under at the moment, etc., the effectors may produce appropriate movements or other responses. However, it cannot be assumed that such will be locomotor, although they clearly are in many cases. They may, for instance, be simply the rolling of an eye or the extension of the dorsal fin. Furthermore, undoubtedly many of the stimulæ may reach no evident effector at all, becoming "lost" in the internal environment with perhaps scarcely a quickened heartbeat. What such stimulæ may have to do with conditioning in fishes we can only speculate upon at present.

The locomotor effectors, the only ones which produce results which can be handled by the present technique, are distinctly axial. That is to say, because of the streamlined shape of a goldfish and its built-in locomotor mechanism, it is much more likely to move forward than in any other direction. While it is capable of backing up, its rising and falling movements are actually, under normal conditions, forward movements deflected up or down and its sidewise movements are forward ones which are laterally deflected. Escobar, Minahan and Shaw (1936) expressed the same thought as follows: "... the locomotor mechanism of fishes (with a few exceptions, e.g., seahorse) are adapted to propel the fish along the axis of the body, the latter being normally oriented in most species of fishes in a horizontal plane."

The Drives. The various internal urges that impel fishes to respond to stimulæ according to certain patterns obviously enter into the locomotor behavior and to a large extent control it. These stimulæ may arrive directly from either the external or internal environment. The seeking of comfort, suitable temperature, light, depth of water, current, contact with solids, which are ordinarily understood as the various tropisms, can be shown to be induced directly by external influences. For the purpose of the experiments many of these may be eliminated by having the factors uniform throughout the experimental tank. Others, such as gravity or light, which necessarily must have some axis, must be allowed for in the calculations. While thigmotropism in its full sense is not a characteristic of the goldfish, its desire to move close to solids is of considerable importance as will develop in some of the experiments.

Lest it might be thought that the agitation of water caused by the passage of another fish tends to keep schools intact, it need only be pointed out that, if fishes are at all aware of such movements, they are entirely inadequate to produce results obtained. As previously mentioned, the obscuration of vision results in the disintegration of schools.

The internal drives of hunger and sex are not easily controlled. By

adequate feeding apparently the first may be neutralized, and by using goldfish out of the breeding season the second may not be important, but as Escobar, Minahan and Shaw (1936) pointed out, "Even in immature individuals sex cannot be ignored, since there may exist dimorphisms and differential physiological abilities." Studies of both these items invite investigation. The above investigators further write: "In the case of animals with highly developed visual sense organs the contour and coloration of their fellows in homotypic or heterotypic groups may conceivably alter their movements resulting in various degrees of aggregation or dispersal." The known attitude of fishes to attempt mating with a variety of quite unfish-like objects does not support this view, however; Lissmann (1932) *Betta splendens* Regan; Breder and Coates (1934, 1935) *Lebistes reticulatus* Peters; Noble (1934) *Eupomotis gibbosus* (Linnaeus); Breder (1936) *Lepomis auritus* (Linnaeus). On the other hand, the abstract of studies by Noble and Curtis (1935) on *Hemichromis bimaculatus* is suggestive of some such differentiation.

Heterotypic schools of fishes are not uncommon and those of young fish are frequently of an ecological nature rather than a specific one, as discussed by Reighard (1915). Parr (1931) considered the temporary sexual dimorphism of *Gasterosteus* as a factor in the breaking up of the earlier non-sexual schools. Breder and Nigrelli (1935a) discussed other cases of heterotypic schools. Perhaps many of the vague controversial matters regarding fish schools and sex recognition could be cleared up by some modification of the technique here used for examining the factors in the simple aggregation of essentially non-schooling species.

The territorial attitude of fishes is well marked in many species, and is associated with tank dominance as has often been mentioned, Breder (1934, 1936). This seems to be strongest in nesting and thigmotropic species and weakest, if present at all, in schooling species. It is at least present to the extent of some aggregations being partial to some small area. Nothing can be said about homing instincts or migratory movements at this time but such would surely only be an influence evident outside of laboratory tanks. The behavior of animals on "home" territory and in unknown country is demonstrably different without the necessity of recourse to the plotting of paths or trajectories.

Spiral Movements. There is a well known tendency for animals when blindfolded or in an environment with inadequate points of reference to move in more or less circular or spiral paths. This seems to be an inherent element of all forms of life examined. Schaeffer (1931) expresses it as follows: "All motile organisms move spirally when guiding senses are not functioning, so far as known. By experiment and observation this has been found to hold true from bacteria to blindfolded aviators." That it is equally true of fishes is subsequently shown. The bearing that this feature has on mass physiology will be discussed in detail at that place. Schaeffer (1928) discusses the general problem of spiral movement and gives a good bibliography. Gordan (1936) detected such movement in the massed flight of insects.

Random Movements. It has been stated by Lotka (1925) that the movements of organisms in a uniform environment should be of a random character. They then follow the Einstein (1905) equation for Brownian movement which is usually given as follows:

$$\Delta_x^2 = \frac{RT}{3\pi N} \frac{t}{\eta\alpha}.$$

Expressed in non-mathematical terms, the law states that the mean squares of the displacement in any direction, in equal intervals of time, is proportional to the elapsed time. This may be expressed graphically by plotting time against the mean squares of the displacements. Then random movement is expressed by a straight line with its origin at the zero point in each axis.

This has been shown to be in agreement with the movements of protozoa by Przibram (1913). Applied in a larger sense to a non-uniform natural environment (in which the irregularities are essentially cancelling) Ross (1923), Pearson and Blakeson (1906), Brownlee (1911), Edgeworth (1920), Cole (1922), Hardy (1922) and others have shown similar phenomena in the migratory or other movements of non-captive organisms. Thompson (1933) has attempted to apply the equation of Einstein to the movements of tagged fishes. Certainly there would be expected to be a large degree of randomness under the conditions of the experiments to be discussed. Consequently by the application of the formula it should be expected to hold, except for the fact that the formula applies theoretically to a space of infinite volume. In the case of small containers and large objects, their early "reflection" back from the sides makes its application unsuitable.

The arbitrary limits of space available made it impossible in our circumstances to use a tank sufficiently large or a fish sufficiently small to apply the Einstein equation directly. However, by certain sub-experiments a fairly clear indication of the relationship of random to spiral movement was obtained which is adequate for the present purpose, at least.

Light, temperature, chemical conditions, objects, and gravitational differential were either controlled or, as in the case of the last, properly allowed for.

The food and sex drives were minimized by adequate feeding and performing the experiments out of the reproductive season. These were clearly sufficiently overcome to give comparable results. Small differential details are explained in connection with the items they modify.

EXPERIMENTAL STUDIES.

The data obtained by various experimental contrivances already referred to in the previous sections are given here in full descriptive detail. The interpretation based upon these results will be found in the section following.

Experiments in Differential Locomotion. For the purposes of this series of experiments a rectangular aquarium 20" x 16" x 14" high was used. This then represented a rectangular enclosure of 4,480 cubic inches. One side and an end were ruled faintly with a glass marking crayon in two inch intervals. The side was thus divided into 70 squares and the end into 56 squares. By viewing simultaneously from the end and side, any fish in the aquarium could be located in any one of the 560 two-inch cubes. Such positions were then noted at ten second intervals for uniform periods. The resulting data, a series of three reference numbers, one for each plane of projection, in a consecutive series (from "0" to "140") could then be calculated in various manners, both as to an estimation of the distance traveled and as to the actual position of the subjects in space. The data, then, which were obtained by all these experiments, are represented by a total of 5,499 points in space, each represented by three index figures or 16,497 projections. Exp. 35 and 36 are omitted because of the partial data taken.

By a suitable geometrical treatment of the data a trajectory of the fish, as measured, at ten-second intervals may be calculated. This, reduced to meters per hour, is given in Table I.¹ Obviously these figures are minimal values as the fishes do not necessarily travel in a straight line between the fairly long intervals. The methods used by Schuett (1934) and Escobar, Minahan and Shaw (1936), give closer approximations to the actual distance traveled. However, our readings were made basically for another purpose and are of course comparable among themselves, giving properly relative values. A study of the data will reveal that there is a very genuine separation between the rate of travel by a fish alone and one with com-

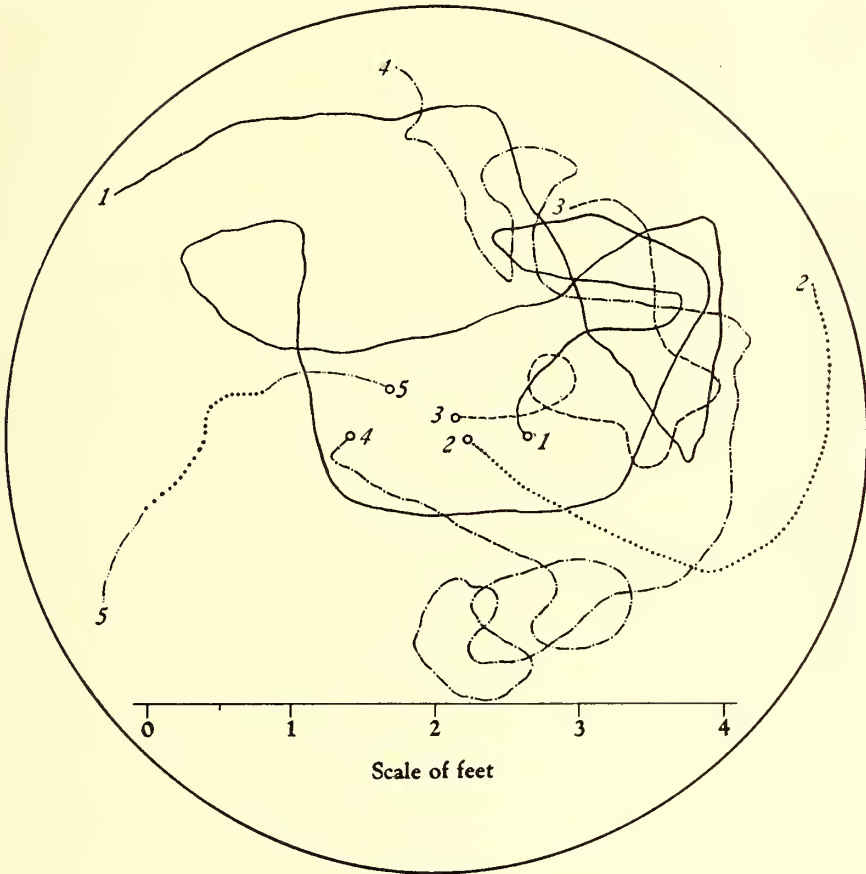
¹ All Tables will be found at the end of this paper.

panions, the details of which are given in the discussion. The first 22 experiments were made by one observer by using a mirror set at an angle of 45° to the ruled end so that both side and end could be observed at one time. This was found to introduce slight complications, either by irregularities in illumination or perhaps by the fish seeing his image. This was subsequently overcome by enclosing the aquarium in a light-tight box, provided with a side and an end "peep hole" and with artificial illumination. This required the simultaneous observations of two people and even here certain irregularities in behavior could be traced to light entering laterally from around the viewing holes. The details of the separate experiments are given in Table I and discussed along with their interpretations.

Another method of handling the data is to consider the fish positions in each plane of projection separately and plot these as frequency curves. Obviously, any correlative changes in the shape of such curves to be found associated with the different conditions indicate a change in the swimming pattern of an active organism. These data are given in Table II. In certain cases it is more convenient simply to consider the aquarium as divided in half of each of its three axes and note the percentage of positions to either side of the mid-lines. These data are given in Table III. Still another way to treat the data is to count the number of crossings of these mid-lines in each plane. This is not the same as the previous treatment as various degrees of activity may give the same distribution or various speeds of travel may include more or less crossings of the mid-lines. Each of the three treatments, however, is nevertheless closely related to the others, and taken together they increase the emphasis on the differential behavior. Still another treatment is to note simply the number of changes in direction and finally to plot out the changes in position along a time axis. These items are considered at this point to indicate the flexibility of the technique rather than for the purpose in hand, the details of which are considered along with the inferences based upon them.

Experiments in Random and Spiral Movements. It is thoroughly evident that the aquarium used in the preceding experiments would be inadequate to make even a cursory study of random and spiral movements in any but nearly microscopic organisms. In order to obtain some estimation of these features a pan six feet in diameter and two inches deep was constructed. The bottom was covered with a uniform layer of sand and the vertical sides were enameled white to make them as little evident as possible under the circumstances. The pan was illuminated from six feet above by four electric fixtures spaced so as to provide a uniform vertical light, and was surrounded by a curtain of heavy white sail canvas to exclude extraneous light and disturbances. A motion picture camera was mounted directly over the center for the production of permanent records. This was found, however, not of any particular value as the experiments developed. The speed with which the fish found the edge of even this pan was so rapid as to give records of little value. It may be noted here that the restriction of the subjects to an essentially two-dimensional field in no way invalidates the calculations. Even a single dimension may be used for such purposes.

Sketch paths of five fish are shown in Text-figure 1. The longest represents not quite 15 seconds, as they were only continued until the subject responded to the side. This was always immediately evident because in every case the subject then began to circle close to it. Table VI gives the details of the data. There is very considerable evidence of typical spiral movements in both the figure and the tabular data. In these five cases the tendency was to turn to the left, resulting in a counter-clockwise traveling about the edge of the pan. These fish were gently placed at the points shown and had never been in the pan before. It was quickly found by a second trial that the conditioning had been such that the subjects learned that there was a sheltering edge not far away if they traveled in any

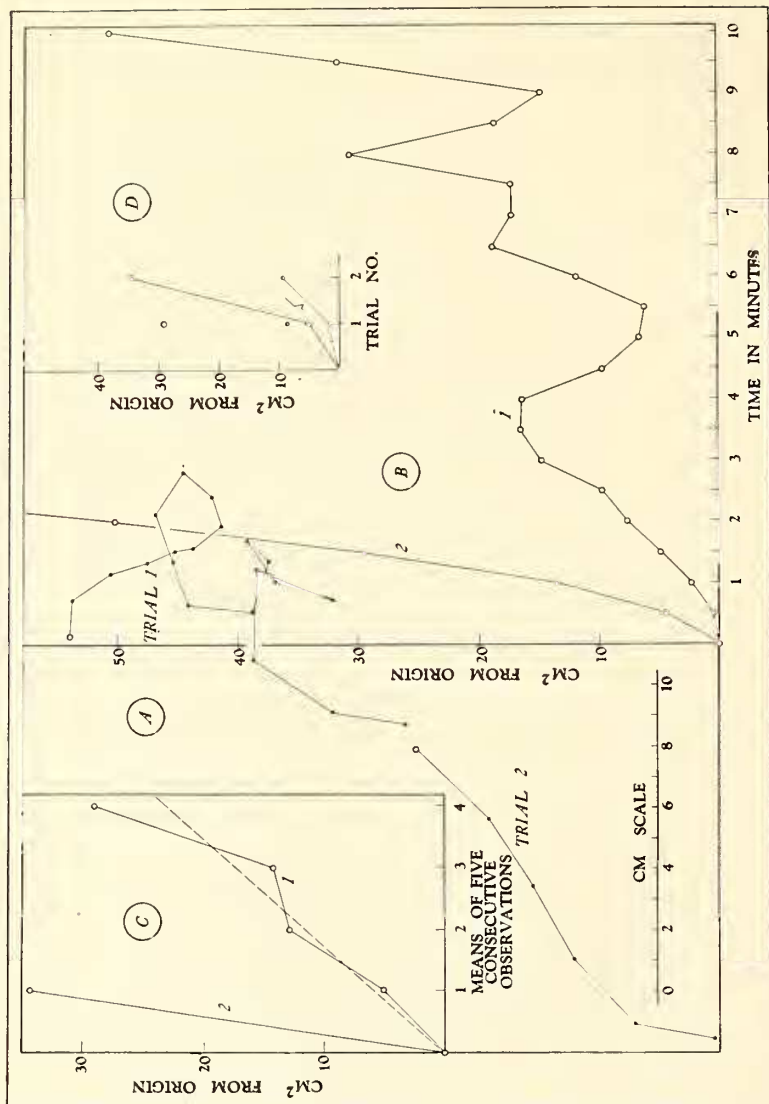


Text-figure 1.

Paths of five fishes of different species in a shallow pan, protected from outside influences. 1. *Carassius* No. 1. 2. *Carassius* No. 2. 3. *Lebistes reticulatus*, female (fish lost sight of at the point shown, but a moment later was found traveling counter-clockwise around edge). 4. *Brachydanio rerio*. 5. *Villariius catus*, 2 cm. long (heavy dotted portion of path picked from a motion picture record, each dot representing every eighth frame or at intervals of $\frac{3}{8}$ of a second). All other paths are free-hand tracings.

straight line. This in itself is rather remarkable, since actual sight of the edge through two or more feet of water is not involved, as is evident from the fact that on second trials they seldom went to the nearest edge but seemingly struck out in a random direction when released but maintained practically a straight path. How this could be we do not yet understand. The short distances at which Breder and Coates (1935) found that *Lebistes* could distinguish even evident objects also bears on this.

After proceeding to this point it became evident that such an apparatus was inadequate for these studies and that suitable equipment was not available, on the basis of space alone, in the laboratories. Because of this, slow moving aquatic gastropods were substituted for fishes as subjects. Their behavior, readily followed, gave some interesting data on animal behavior, which would seem to be in accord with what the preceding fragmentary

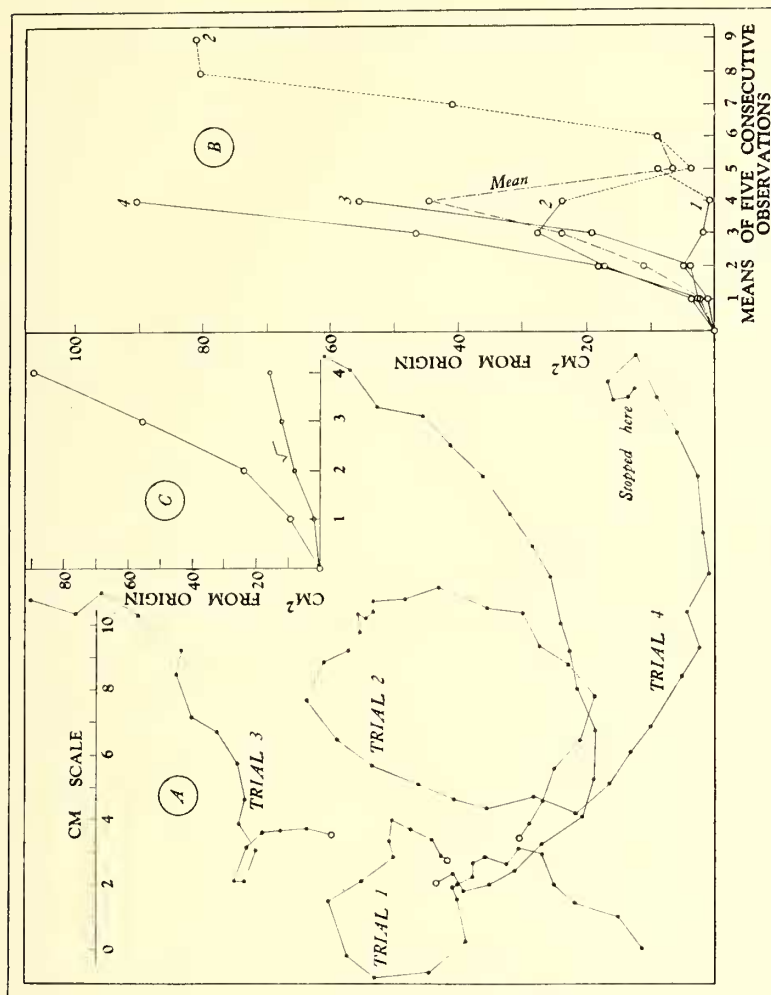


Text-figure 2.

Paths of *Physa*. First and second trials of snail No. 1 with resulting data plotted three different ways. **A.** Actual paths of trial 1 and 2. **B.** Square of displacements plotted against time. **C.** Means of five consecutive observations plotted as in "B". **D.** Mean positions and their square roots at the end of periods given in "C". The connected points correspond to the first period. The unconnected points correspond to the fourth, as there are no data for this from the second trial.

experiments would lead us to believe. Fortunately for the work, the snails all seemed dissatisfied with a position on a flat horizontal surface and showed a strong disposition to come to rest on the vertical sides of the pan. The only difference in physical equipment was the placing of a large piece of French plate glass over the sand so as to give the creeping snails an absolutely plane surface to move over. Under this was inserted a pale gray piece of cardboard, pencil ruled in small, scarcely discernible, squares.

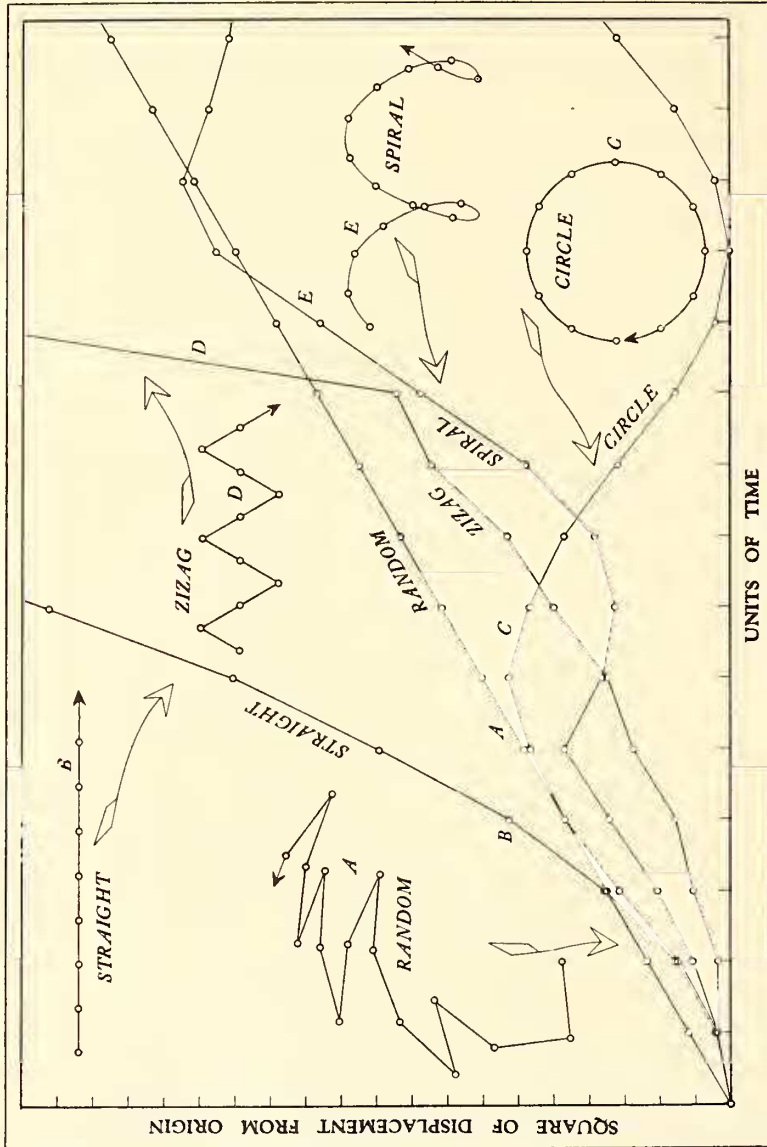
The trial paths of certain snails are given in Text-figures 2 and 3. Here, too, there are undoubted spiral movements, but the bias is slightly to the right. The behavior of these snails yielded further data bearing on the subject of random movement which is not entirely clear at this writing. It was found, for example, that the first trial of *Physa* No. 1 was much more nearly random than the second. The actual paths of these two trials are



Text-figure 3.

Paths of *Planorbis*. First to fourth trials of snail No. 1 with data plotted two different ways. **A.** Actual paths of trials 1, 2, 3 and 4. **B.** Means of five consecutive observations plotted as in Text-figure 2, C, as well as the mean of the four trials. **C.** Mean positions and their square roots at the end of periods given in "B".

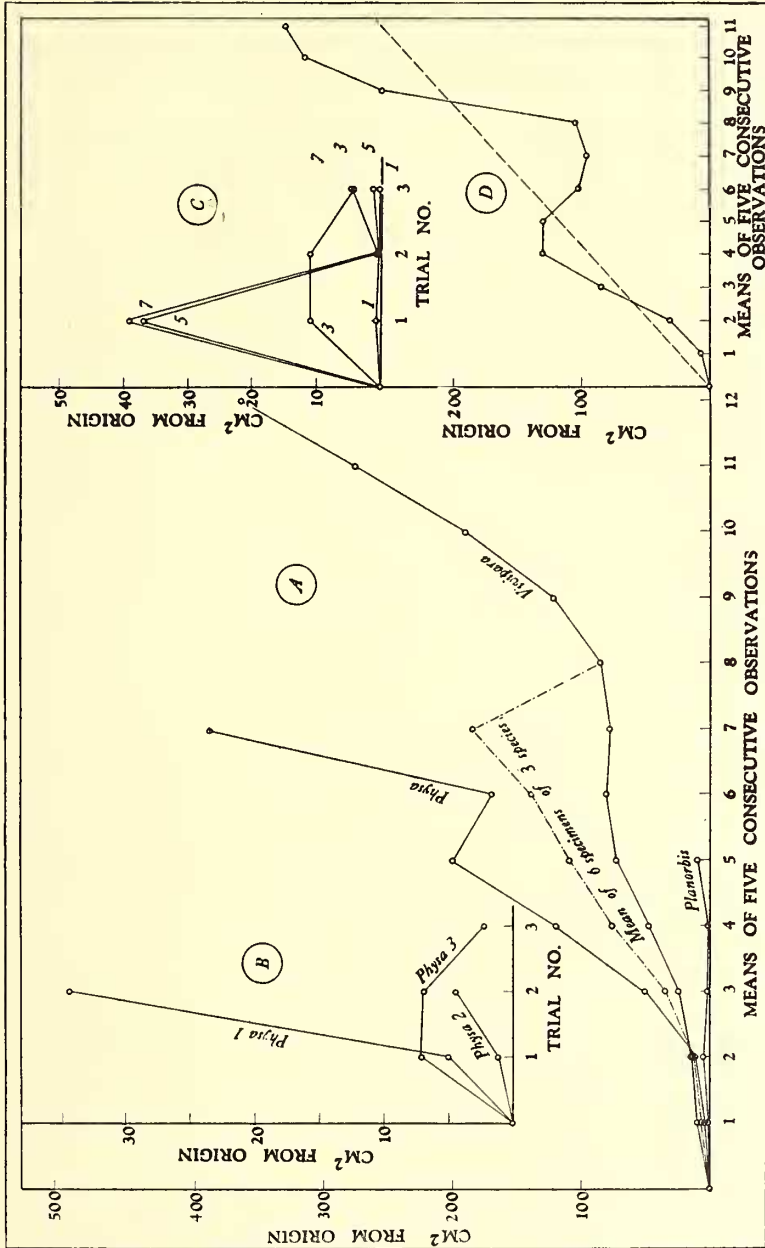
given to Text-figure 2A. The data of these, plotted according to the Einstein equation (i.e., square of the distance from the origin against time), are also shown here and indicate that the second more closely approximates that of a straight line while the first more closely resembles that of a spiral path (Text-figure 2B). See Text-figure 4 for illustrations of typical lines of translation and their representation by this type of plotting. If the means of 5 consecutive points be plotted, curves are obtained which are given in Text-figure 2C. Of the second little can be said because of the slight amount of data, although it is obvious that this line must become more and more nearly a straight one as the quantities taken to obtain mean values are increased. The first path in this graph also more nearly approaches a straight line, for similar reasons. The angle of these lines to the horizontal gives a measure of the speed of recession from the origin and insofar gives a measure of the behavior of the organism. At this point a difficulty inherent in the method becomes apparent, since by an appropriate selection of mean values a given path such as the first can be either represented as indicating a spiral movement or a random movement. This is not so serious as it might



Text-figure 4.

Geometrical paths and their representations in graphic form for comparison with Text-figures 2, B and C; 3, B; and 5, A and D. The indices indicate uniform units of time against squares of displacement from origin. The resulting curves are reduced to one-half the scale of the originating paths. **A.** Random movement. **B.** Straight path. **C.** Closed circular orbit. **D.** Zigzag path. **E.** Spiral path.

be first thought, since what it actually indicates is that elements of both are present and either one may be emphasized and studied according to the scale of operations under consideration. This seeming paradox becomes clear when it is considered that an animal or other object may be cutting close spirals, turning cart-wheels or showing other vagaries of locomotion and still be moving in a random fashion, if considered in a larger sense. On the other hand an animal may be moving in very large spirals on which are overlaid a measure of randomness considered in a finer sense. This only becomes confusing when the size of the spirals and the random paths are of similar magnitudes. However, it is just in such cases that the value of this approach is greatest.



Text-figure 5.

Resultant calculations from paths of *Physa*, *Planorbis* and *Vivipara*. A. Mean paths of all individuals studied by species plotted as in Text-figure 2. B. Mean positions at the end of periods of three specimens of *Physa*, plotted as in Text-figure 2. C. *Physa* No. 3 at the end of periods 1, 3, 5 and 7, indicating the inability of this individual to "learn"; compare with "B". D. Mean of three trials of *Physa* No. 3; compare with Text-figure 2, B and C.

The underlying biological causes of these differences between the snail paths No. 1 and No. 2 are not so evident but would seem to have their roots in some conditioning, orientation, or more broadly some learning process. By plotting the data still another way (i.e., trial number against distance from the origin at the end of fixed periods), what may tentatively be called a learning curve is obtained. This is given in Text-figure 2D. Further data of other individuals of *Physa* are given in Text-figure 5. The learning curves

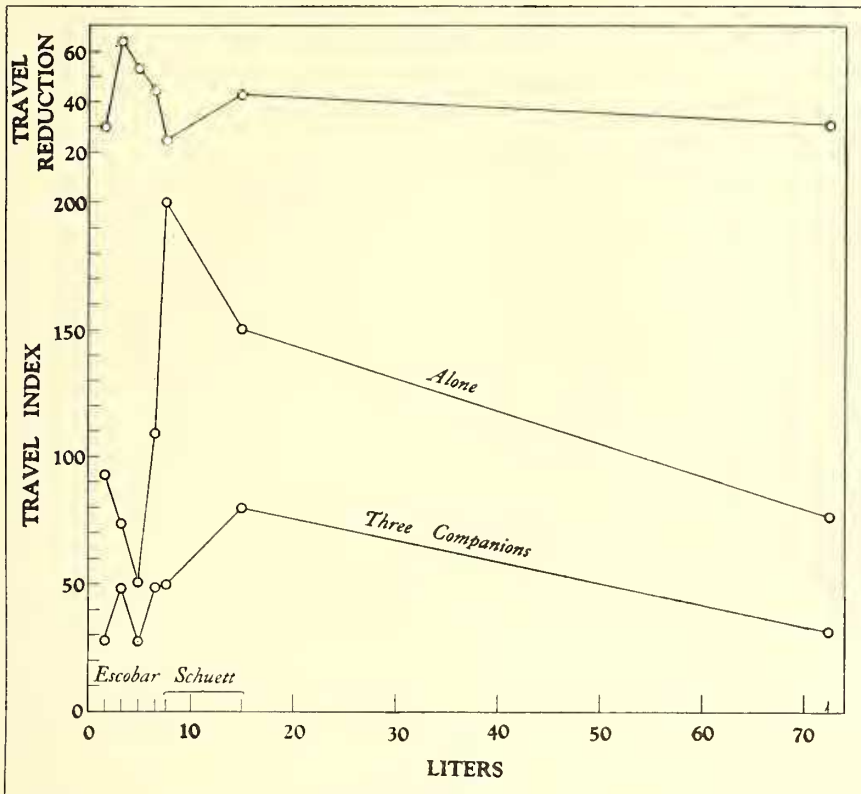
of three specimens show considerable differences, including one individual which apparently failed to learn, performing more poorly on each successive trials (Text-figure 5B). However, it is clearly evident that the mean of these three snails nevertheless shows some shift to an increasing speed of recession from the origin on successive trials. These observed differences may be due to individual background or other factors in the life of the animals. Text-figure 5C shows the positions of *Physa* No. 3 at the end of four different periods in each of its three trials, again indicating its lack of learning. The essential random and spiral nature of the paths are also indicated in Text-figure 5D in which the mean trial of the *Physa* No. 3 shows a marked resemblance to the first path of No. 1 given in Text-figure 2B. The means of all trials of these three *Physa* are likewise given, which emphasizes the characteristics common to all of them (Text-figure 5A).

Data on another species, *Planorbis*, are given in Text-figure 3 and show similar characteristics. The actual paths are given and the resulting plottings. The mean of four trials shows again the spiral and random tendencies inherent in these paths. The learning curve is well marked and, as in the other species, is shown both with the data as picked from the curve and the square roots of those values.

Similar studies of two specimens of *V. vivipara*, the data of which are not given in full, appear in the mean values for all in Text-figure 5A. This species was added to the previous two, since it is not a pulmonate. The essential similarity of its behavior is evident. The difference in shapes of the curves of the three species is referable directly to their activity and speed. It is to be noted how basically similar are all patterns.

SIGNIFICANCE OF OBSERVED BEHAVIOR.

The data obtained by means of the experiments previously described and presented in Tables I and V in most cases may be better understood if presented in graphic form. The index of the rate of travel under various conditions as expressed by the data of Experiments 1 to 22 of Table I is analyzed in Table IV. It may be seen at once from this table that the two fishes tested move much faster when alone than when with companions. This holds not only for the mean values obtained but also for both the maximum and minimum values. It is also to be noted that there is but one case of overlapping of extreme figures and that there is virtually complete separation between the two sets of values. Actually this is strictly true for all of the mean values, the only ones of full statistical significance. Maximum and minimum values show a separation of over 50% and the minimum considerably more. The close agreement between the two test fishes is to be especially noted. These data support the experiments of Schuett (1934) and Escobar, Minahan and Shaw (1936). The data of these investigators are given in Table III. This has been equated as well as is possible from their data to the present experiments. Since, however, their procedure differed somewhat from the present it cannot be thoroughly comparable, although it is fully adequate to establish the validity of the increase in speed of travel in *Carassius* with solitude. These data are presented in graphic form in Text-figure 6. Some of the irregularities are doubtless due to differences in technique and methods of calculation. This is largely obviated in the top-most line which represents the travel of a fish with companions as a percentage of the fish alone. The apparent differences smooth out to a considerable extent under such treatment, well indicating the basic agreement between the three sets of studies. Lest it may be thought that the different O₂ and CO₂ concentrations associated with various numbers of fish are responsible for these differences it is but necessary to point out that Schuett (1934) successfully ruled out this factor for a much smaller aquarium than the one here used.



Text-figure 6.

Comparison of the data of Schuett (1934), Escobar, Minahan and Shaw (1936), with the present. The topmost line was computed by reducing the amount of travel of the fish alone to unity. Then the indicated figures represent the extent of travel reduction with three companions.

The new experiments, each representing a special feature that in some cases shows more clearly just what transpired by other treatment of the data, may be now considered in reference to rate of travel. Another fish, "C", in the shadow box (Exp. 23) previously described and illuminated by a hundred watt light, showed a speed of 162.15 M/h when alone. The addition of other fish (Exp. 24) one-half hour later resulted in even a higher rate of travel (166.98 M/h). These fish changed abruptly from daylight were clearly worried and it would seem that their rapid movements were responsible for the failure of the accommodated test fish to reduce its speed. Further data on this appear in the consideration of the effect of light. Later, on the removal of the box (Exp. 25 and 26), the travel reduced to values comparable to those of "A" and "B" with companions; 61.70 and 33.39, mean 47.54.

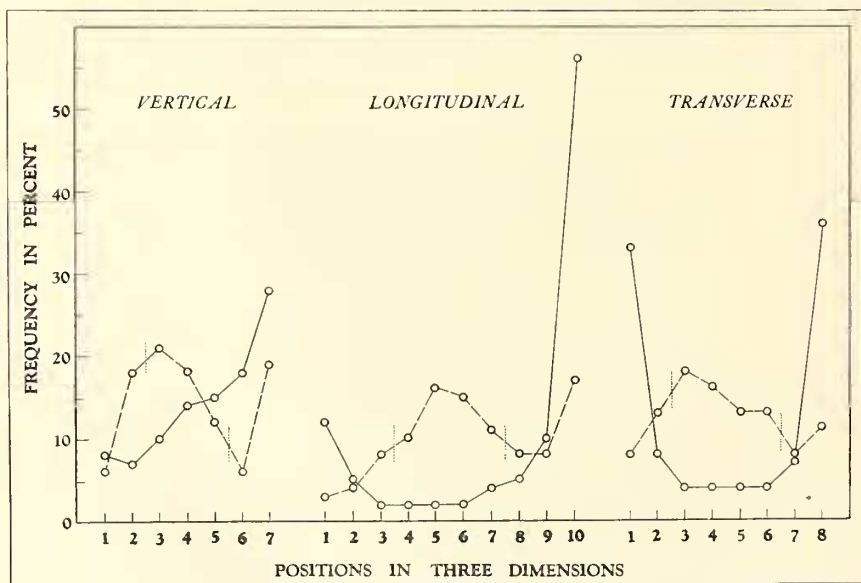
A rotating motor-driven disc placed under the electric bulb, causing the rapid passing of shadows, clearly caused fright and the speed increased (Exp. 27). Some hours later this was even higher (Exp. 28) and three days later (Exp. 29) the speed was still high although it is hard to imagine that this effect lasted that long. This feature needs further study.

Another fish, "D", was then studied in relation to the amount of light

used. The data are given in Experiments 30 to 35. If the values of fish alone are plotted, there seems to be an increase of speed with an increase of illumination but the data are inadequate for a thorough understanding of this phenomenon. The other items cannot be elucidated in terms of speed of travel at this time but are discussed in subsequent connections.

The distribution of the experimental fishes in space is given in Table V, expressed in terms of percentage. If again the first 22 experiments are combined their mean distribution alone and with companions may then be plotted and compared. These calculations are given in Table V and the resulting graphs are shown in Text-figure 7. It will be noted at once that the curves obtained from fishes alone are convex downwards and those from fishes with companions are convex upwards. An examination of the data of Table II will show that this is a consistent feature of each experiment. The separation is not so clear in some individual cases as in the integrated means of Text-figure 7, but in each of these there is a reasonably clear and evident reason because of the conditions of the experiments and to that extent forms a measure of the particular influences at work as noted in Table I. The minor distortions of the curves of Text-figure 7 are each indicative of tendencies in the subject and form an excellent quantitative measure of them. A consideration of the curves in detail yields the following data, each treated according to its separate coordinates.

The vertical curve of the fish alone shows that the fish tended in a regular manner to keep close to the bottom of the aquarium. Actually it occupied the bottom 2" of water 28% of the time and the surface 2" only 8%, with a quite regular grading of the intermediate strata. Considering the 14 individual experiments upon which this curve of the fish alone is based, there are the following extreme divergencies: Percentage of time



Text-figure 7.

Configurational behavior of goldfish alone and with companions in respect to three dimensions. Solid line: fish alone. Dotted line: fish with three companions. The short vertical pecked lines on the latter indicate the limits, counting from the central position that covers 50% of the readings. A projection of these on the solid line shows that over 50% is there excluded by them instead of included.

spent in the bottom layer varied from a minimum of 13% to a maximum of 60% while time spent in the surface layer varied from a minimum of 0% to a maximum of 31%. In only three of the experiments did the fish spend more time in the surface layer than in the bottom one, and in only one was a peak value reached in the middle layer. This may simply be taken as a mathematical expression of the normal attitude of a solitary *Carassius* as based on casual but extensive observations, to the effect that they are apt to be found near the bottom, and if not there, at the surface, and least commonly in mid-water.

If now the curve of the fish with companions be considered, it is clear that a considerable change in distribution has taken place, the peculiar S-shape of the curve apparently indicating two loci, or that the fish is hesitant between two sites of approximately equal preference. The bottom layer accounts for 19% of the time while an intermediate layer of from 6" to 8" from the surface accounts for 21% of the time. The surface layer is visited about as frequently as before (6%), but the distribution between surface and bottom is utterly different. Over 50% of the time is spent in layers 2, 3 and 4 (57%); the small values of the layers below these, except the bottom one, indicate rapid dashes through them to cruise along in the latter. With the same fish alone over 50% of the time was spent in layers 5, 6 and 7 (61%). If we divide the tank into a top and bottom half it appears that alone the fish spent 68% below and 32% above such a mid-line. With companions this was inverted to read 54% below and 46% above, indicating a more nearly uniform distribution.

The "longitudinal" curve running at right angles to gravity shows a strong tendency for the solitary fish to keep to either end of the tank, most markedly so at the right end. This was the end at which the mirror stood and the curve gives a measure of the attractiveness of this device. If it may be assumed that either end was equally attractive except for the mirror, then the difference of the readings at either end ($56 - 12 = 44\%$) may be taken as a measure of this attraction. When companions are added and a more median position is selected, as evidenced by the shape of the curve, the strong attraction for the mirror end reduces but does not disappear. Thus, between the two sets of experiments the attractiveness dropped from a value of 56% as compared with all other influences in this plane to one of 17% on the addition of three companions. The non-mirrored end dropped from 12% to 3% and since the latter is the lowest value on the curve, presumably indicates that its attractive value fell to zero. The median positions 3, 4, 5, 6 and 7 account for 60% of the time, whereas when alone the terminal position 10 accounted for 56% of the time.

The "transverse" curve is essentially similar to the longitudinal one and with fish alone either side seemed to be equally attractive (33% and 36% respectively). Since there was no differential as in the longitudinal measure, this is what one should naturally expect. The addition of three companions caused the sides to lose their relative attractiveness to the extent that the four central coordinates, Nos. 3, 4, 5, and 6, accounted for 60% of the time.

Dividing the transverse measures in half, we find that alone the distribution to left and right is 49% and 51% respectively and with companions 55% and 45%. These differences are likely too small to be significant and seem to indicate merely the degree of accuracy obtainable by this method on a half and half distribution. If, however, we take the longitudinal measure and handle it in the same way, the figures for the fish alone stand left 23% and right 77%. With companions this becomes 41% and 59%. The bias by the mirror in this is thus overcome by the introduction of three fish to the extent above indicated. The biological significance of the basic distortion of the spatial distribution curves of these fish with and without companions is quite apparent. The interpretation of them would seem to be somewhat as follows: Since goldfish are gregarious, the behavior re-

flected in these curves is evidently a measure of this social disposition. The species may be said to be an aggregating one but not a schooling one in the restricted sense, as may be checked by reference to goldfish in a fairly large pond. The exact behavior in a small aquarium, however, because of its limitations of space, can only be properly appreciated by some such treatment as the present. With these considerations in mind it would seem that both the increased speed of travel and the tendency to seek the walls of the aquarium would be due to an attempt to find company. This finding of company with the resulting slowing down of movement and the formation of an aggregation remote from the aquarium walls would then indicate a satisfaction of that drive. Since the aggregating tendency implies an urge to seek a position close to but not in contact with some object (another fish), it also may be that approach to some inanimate object or surface is used as a substitute to partially satisfy that urge when no companions are present. In fact, it may even be that the movements of the other fish is the determining factor in the expression of the preference of approach to a fish as against a surface. It must be borne in mind, however, that the glass walls of the tank are optically not very evident. If other sensory organs enter here they are not yet evident, for as previously mentioned the fish school in general appears to be a purely visual affair. The fact that aggregations form remote from the walls is not surprising on a purely mechanical basis. If each fish is considered as having a "field" of influence about it, the formation of the aggregation in mid-water would be expected. Fish in a central position would exert the effect of their presence at every point on the surface of a sphere at whose center they were located. Fish close to a side could exert only one-half that, i.e. on the surface of a hemisphere. Fish at the junction of two sides would exert a quarter as much and one in a corner one-eighth as much for similar reasons. It is not necessary to labor the point that such objects, moving either primarily at random or in spirals and mutually affecting each other, would aggregate at approximately the tank center equi-distant from the sides. Divergence from this would then indicate other influences.

If a space is enclosed that includes 50% of the positions, counting from the center both ways, Text-figure 7 indicates that it also includes the peaks of each of the curves of the fish with companions. Short vertical lines show these limits in that figure. These lines projected to include the curves of fish alone for the longitudinal and transverse readings include a very small percentage, i.e., 10% and 16% respectively. That for the vertical component is somewhat different because of the fact that it is at right angles to the main axis of the fish and parallel to the gravitational field. Here the curve of the fish alone is a gradual increase from one end to the other and the corresponding value is intermediate between the one on either side, i.e., 15%, 39%, and 46%.

Schuett (1934) in considering the speed of movement alone has shown that there is some optimum of crowding above and below which the fish move with greater rapidity. This would seem clearly to be for the reasons above outlined. Since these fish place themselves in regard to one another at some "standard" distance, the findings of Schuett would naturally follow and the whole phenomenon become one of seeking an equilibrium. Fast random swimming certainly would tend more quickly to restore a "lost" goldfish to its group as well as tend more quickly to disperse an aggregation too closely packed for comfort.

Having considered the primary significance of the configurational distribution of fishes, the details of the further experiments may be discussed. Experiment 23 made in the shadow box alone shows much greater equality of distribution at either end of the horizontal components; longitudinal 32% and 22%, transverse 32% and 28%. Here the confusing outside elements were eliminated, giving another evidence of the influence of the end

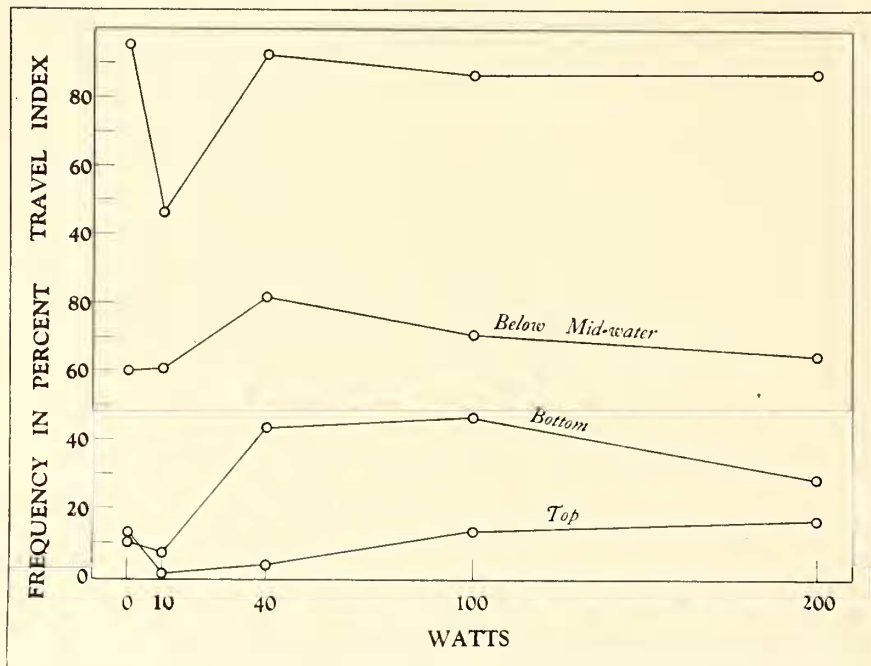
mirror of the 22 primary experiments. The vertical component was in essential agreement with the previous, the surface layer .01% and the bottom and highest figure 37%. This agreement is surprisingly close when it is considered that this single experiment was only 1/22 as long as the mean values previously discussed. Experiment 24 showed no change in speed, as previously noted, and agreeing with this it also showed no change in configuration. The presumed reason has already been mentioned, but it may be pointed out that the rate of speed and configuration of pattern are clearly not locked to each other on any mechanical basis. Consequently in the present case we have two separate approaches, both of which indicate that in this set of two experiments the expected response to companions that has already been established here and by others did not take place. Experiments 25 and 26, without the shadow box, showed irregularities not unlike those of the earlier experiments. As the speed of the fish slowed down, as previously noted, the configuration took on an approach to that of fish "A" and "B" with companions. All that can be said of this is that fish "C" either responded more slowly to companions or was simply not as reactive. Perhaps this could eventually be shown as a matter of individual difference in the "psychic" attitude of various goldfish.

The light was then interrupted (Exp. 27) and the fishes sought either end of the tank, spending 28% and 29% of the time in the two end divisions. The next day (Exp. 28) they returned to a more nearly normal distribution, the ends receiving only .08% and 19% of the positions.

Fish "D" with three companions (Exp. 30) behaved in a normal fashion. This fish was then tested alone with various degrees of illumination (Exp. 31 to 35). The results of this can be best understood by an inspection of Table V. Experiment 35, with a very faint light, just enough to enable the making of the necessary observations, showed the fish to have spent much time in mid-water. The three central coordinates accounted for 57% of the time. Experiment 31, with a 10-watt bulb, showed a considerable resemblance to this one with the same coordinates accounting for 66% of the time. These are the only two readings obtained with vertical characteristics of this nature and they are the two most weakly illuminated ones. This again suggests the visual nature of the movements and aggregating behavior in these fish. The other three experiments (32, 33 and 34) with 40, 100 and 200-watt bulbs all showed a strong predilection for the bottom, but the data cannot decide if there is a gradual change with increased illumination or whether it is simply a matter of passing some threshold. Text-figure 8 gives this data graphically. It is to be noted that in case of "no illumination" the fish spent more time in the top layer than in the bottom. The various elements of this figure, including that of speed, would seem to indicate that the lack of light was stimulating to locomotor activity but without any configurational influence, that a low illumination (10 watts) was quieting but again with no influence on the configuration, but that a higher illumination (40 watts) drove the fish sharply to the bottom and increased the locomotor activity. Increase of illumination above this point seemed to have very little effect, but seemed, if the figures can be trusted to such details, not to hold the fish so closely to the tank floor. It is doubted if such slight differences are significant, however. If anything, it would seem that there may be an activity and behavior threshold somewhere between the illumination of the 10 and 40 watt lamps.

Experiments 36 and 37 represent the simultaneous paths of "C" and "D". For practical reasons they could be taken in two ordinates only. The extent of agreement is close, but no closer than the agreement between successive observations on the same fish. Consequently it is inferred that these observed differences of such order are due to inherent variant characters in the fish rather than unrecognized extrinsic elements.

A fifth fish, "E", was tested in Experiments 38 to 41. The four fish,



Text-figure 8.

Behavior of goldfish in respect to vertical distribution under different amounts of illumination. See text for explanation.

A to D, which were examined at other times, were the companions of the test fish. The speed of travel under varying light conditions was less with companions than without, but the separation was not as great as in "A" and "B". The configuration, however, was in quite good agreement.

Another method of measurement of such activity is to plot the actual transit of the mid-line or to check the reversals of direction. The amount of labor involved in such calculations, however, is disproportionate to the results, which so far as can be seen from the present data give no further information than that already obtained from the more readily applied methods herein discussed.

An attempt was made to calculate the displacements according to the formula of Einstein (1905) for random movement, but it soon became apparent that the small size of the vessel in relation to the size and movement of the fish made it impossible of application. The thesis was taken that if such a fish moved at random, then any diversion from such randomness could be used as a measure of mental integration on the part of the fish. It is now clear, however, from a study of the movement patterns, that in any case such behavior is not of a fully random nature, but is at all times guided by a series of integrated perceptions, however slight.

Since the formula for Brownian movement, which may be used just as well in two dimensions, is so closely controlled by physical influences, recourse was made to the use of a large, shallow pan, virtually of two dimensions, employing much smaller fishes. Here, too, we encountered a difficulty, much different in nature, but one which finally led to the use of aquatic univalves. A description of this device is given in the experimental section together with the results obtained. The interpretation of these data involves the further confirmation of the tendency of organisms to travel in spiral

paths when there is an absence of "landmarks" to guide them. The simultaneous action of the innate tendency to spiral and move in a broader sense at random has been fully set forth in the experimental section. That this is readily modified by some sort of "learning" is also apparent from the experiments. Whether this is associated also with an obscure means of orientation similar to that of "homing" as found in many animals or simply that the snails were impelled by some drive is not fully clear. We suspect that it is the latter, however, for when left alone all three species came to rest on the vertical sides of the pan. The pulmonates had evident reason, but it is not clear in the case of the branchiate form. If the snails could detect these vertical surfaces at such a distance it is most surprising. That the re-crossing of their previous paths had no bearing on the subject is evident from the actual paths shown in Text-figures 2 and 3, as some did not cross at all and where they did there is no evidence of significant change of direction.

The points that these considerations bring out enable us to determine the minimum requirements for an adequate study of the phenomenon involved: 1. A vessel must be used in which it is possible for the organism to do considerable random and spiral wanderings without being able to "pick up" any landmarks. This may be a "two dimensional" space if necessary. For any animals of microscopic size the physical limitations of most laboratories present difficulties. 2. Photographic recording at suitable time intervals would be practically essential for any extensive survey of this field. Since neither space, time nor suitable equipment are available to us under present circumstances it was deemed best to indicate the progress of this work in the hope that someone better situated would be able to further it.

The fundamental nature and reasons for the existence of these spiral movements have been speculated on by various investigators, chiefly Schaeffer (1928). According to our views, certain features of them may be thought of in terms somewhat according to the following: It has been shown for invertebrate animals that those which move by means of muscular effort as opposed to ciliary efforts, behave differentially under various amounts of illumination (Welsh, 1933). The former move more rapidly, according to their phototropism, as the units of illumination are increased, while the latter show no such correlation. The present studies indicate a greater amount of movement under an increased illumination at right angles to the plane of activity. This suggests a similar increase in muscular effort under such stimulation in at least the lower vertebrates. It should follow from this that such spiral movements as may be present would tend to become exaggerated. Since the muscular efforts are being intensified, their unit acts come at shorter intervals and a given path is covered in a shorter period of time. This would seem to culminate in the spiral paths of insects about strong lights or even in the extreme conditions in some fishes discussed by Breder and Harris (1935). These remarks are undoubtedly an over-simplification of the condition, a more full examination revealing that a number of separate items enter into the complex of behavior, at least including the following:

1. Increasing speed of translation with increased illumination.
 - a. Direct positive or negative phototropism (Welsh, 1933).
 - b. Movements at right angles to axis of light (original).
2. Spiral movements inherent in organisms (Schaeffer, 1928, and others).
3. Tendency to expose dorsum (or other surface) to source of strong illumination (Breder and Harris, 1935).
4. Disturbance of neural integration by large changes in illumination (Breder and Harris, 1935).
5. Disturbance of neural integration by other environmental or pathological causes (Hollister, 1934).

It is not necessary for certain effects that all of these factors be present in evident form and there may be still others, as yet unanalyzed. As far as it is possible to understand these effects at present it would seem that the increasing speed of normal reactions to light due to increased illumination and the inherent tendency for organisms to show circling movements are basic to the rest and represent all that is necessary to account for them. The resulting movements from slight stimulæ may be of value to the individual, but beyond a certain point may lead to destruction.

It is evident from many quarters that the social relationship of a fish to its companions is not static but changes rather violently from time to time. Among adults this is most evident during the reproductive cycles as is emphasized in practically every paper on fish reproduction. Even in immature fish diverse influences are at work. Most recently this has been emphasized by Langlois (1935), who studied the relationships between young bass in fish-rearing ponds. Not only did he find that changes proceeded with their development, but that quite different associations appeared in ponds that were essentially similar in environment and original population. This he treated by measuring the output at the end of the season. From some he obtained a uniform group showing only the normal curve of variation in which all fed on the food supplied. In others he found a group of small fish and a group of large, the latter feeding on the smaller and refusing other food as well as showing different attitudes toward schooling. In all he enumerated eight different types of social organization, all derived from similar starting points. This is mentioned to emphasize the dynamic quality of fish aggregations and to indicate to some extent that the problem cannot be handled as one involving only the varying aspects of a continuing attitude on the part of the subjects involved.

Welty (1934) studied the learning of a maze by goldfish with and without companions that had been trained in the same maze. He found that those with trained companions learned the maze faster. The aggregating tendencies of this species certainly account for his results, as indeed might be expected. The results give a measure of the influence of an individual that "knows" where it is going over one that does not.

SUMMARY.

1. The relation of swimming speed to the number of fishes present as indicated by Schuett (1934) and Escobar, Minahan and Shaw (1936) has been further confirmed in larger bodies of water.

2. The mean positions of fish in relation to coordinates in three dimensions is shown to be modified by the numbers present in a significant manner, providing a quantitative technique for the study of environmental influences in active animals.

3. The inherent tendency for animals to travel in spiral paths has been shown for fishes and snails.

4. The essentially random nature of the broader movements of animals has been indicated, as have been the experimental requirements for its full study.

5. The equation of Einstein for the movement of Brownian particles should be applicable to the higher organisms if proper data could be obtained.

6. The basic nature of the tendency of organisms to travel in spiral paths may be influenced to various degrees by impingement of the environment on the neuro-mechanism and can be shown to reach from useful activity to self-destruction.

TABLE I.

Data on extent of locomotion and conditions of experiments. *Carassius auratus*, 2 to 3 inches. Each experiment covers 140 observations. Aquaria 20 x 16 x 14 inches high (50.8 x 40.6 x 35.6 cm.). Volume 4,480 cubic inches (72,427 cc.).

No.	Date.	Hour of Start.	No. of Companions.	Meters per Hour.	Condition.	Remarks.	Fish.
1	Aug. 21	1:45	0	72.96	Open tank with mirror.	{ One continuous reading.	A
2	Aug. 21	2:05	0	76.39	Open tank with mirror.		A
3	Aug. 21	2:25	0	87.20	Open tank with mirror.		A
4	Aug. 22	11:20	0	101.45	Open tank with mirror.		A
5	Aug. 22	1:55	0	93.60	Open tank with mirror.		A
6	Aug. 22	4:30	0	84.20	Open tank with mirror.		A
7	Aug. 27	9:30	3	27.98	Open tank with mirror.		A
8	Aug. 27	1:05	3	38.45	Open tank with mirror.		A
9	Aug. 27	4:00	3	26.45	Open tank with mirror.		A
10	Aug. 28	9:35	3	42.37	Open tank with mirror.		A
11	Sept. 5	3:10	3	17.17	Open tank with mirror.		A
12	Aug. 27	2:55	3	50.70	Open tank with mirror.		B
13	Aug. 28	10:00	3	34.38	Open tank with mirror.		B
14	Sept. 5	2:00	3	14.91	Open tank with mirror.		B
15	Sept. 5	4:30	0	49.38	Open tank with mirror.	{ 15 min. after companions were removed.	B
16	Sept. 6	9:25	0	70.12	Open tank with mirror.		B
17	Sept. 6	3:30	0	78.85	Open tank with mirror.		B
18	Sept. 7	9:05	0	58.45	Open tank with mirror.		B
19	Sept. 7	1:35	0	68.35	Open tank with mirror.		B
20	Sept. 8	11:15	0	62.50	Open tank with mirror.		B
21	Sept. 10	11:25	0	81.59	Open tank with mirror.		B
22	Sept. 11	11:00	0	89.48	Open tank with mirror.		B
23	Apr. 13	10:30	0	162.15	In box. 100 Watts.		C
24	Apr. 15	11:00	3	166.98	In box. 100 Watts.		C
25	Apr. 18	2:00	3	61.70	Out of box. Daylight only.		C
26	Apr. 19	11:30	3	33.39	Out of box. 40 Watts.		C
27	Apr. 19	12:00	3	63.35	Out of box. 40 Watts. (Rotor).		C
28	Apr. 19	4:30	3	91.95	Out of box. 40 Watts. (No rotor).		C
29	Apr. 22	2:30	3	79.48	Out of box. Daylight only.		C
30	Apr. 18	3:00	3	34.49	Out of box. Daylight only.		D
31	June 4		0	46.49	In box. 10 Watts.	Simultaneous with 37. Simultaneous with 36.	D
32	June 5		0	92.85	In box. 40 Watts.		D
33	June 6		0	86.95	In box. 100 Watts.		D
34	June 7		0	87.48	In box. 200 Watts.		D
35	June 10		0	95.10	In box. (No light).		D
36	Apr. 22	3:10	1	Out of box. Daylight only.		C
37	Apr. 22	3:10	1	Out of box. Daylight only.		D
38	Apr. 22	4:10	0	78.45	Out of box. 40 Watts.		E
39	Apr. 23		0	110.2	In box. 100 Watts.		E
40	Apr. 26		3	52.49	In box. 100 Watts.		E
41	Apr. 26	3:10	3	103.1	In box. 40 Watts.		E

TABLE II.

V, vertical index from top down. **L**, longitudinal index from left to right. **T**, transverse index from front to back. Numbers under **Position** indicate each 2-inch space of projection. Figures in body of Table equal percentage of period occupied.

Experiment.	1			2			3			4			5			6		
Position.	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T
1	15	07	59	20	08	88	16	04	93	22	05	62	31	04	09	09	09	25
2	09	05	11	18	11	08	26	06	05	19	05	06	09	11	09	02	04	09
3	13	04	08	13	02	04	11	07	02	11	05	01	13	01	05	08	03	06
4	11	03	04	07	02	00	14	02	00	08	03	05	13	05	05	04	04	09
5	11	03	04	08	04	00	13	01	00	13	02	05	08	05	03	08	02	09
6	14	01	04	11	01	00	06	04	00	09	01	05	13	01	08	09	04	06
7	27	01	05	23	08	00	14	04	00	18	06	06	13	03	13	60	13	10
8		03	05		04	00		06	00		10	10		06	48		18	26
9		13			15			15			13			13			15	
10		60			45			51			50			51			28	

Experiment.	7			8			9			10			11			12		
1	07	04	20	06	05	09	12	10	08	10	05	23	01	00	03	00	00	03
2	19	01	10	13	02	21	10	17	28	27	07	24	14	02	02	05	00	07
3	25	00	20	14	21	37	14	07	16	19	21	14	36	01	13	12	00	05
4	23	09	20	19	18	05	23	12	14	10	13	19	18	13	19	17	00	09
5	10	25	12	18	22	16	07	17	10	05	09	12	20	20	25	24	00	05
6	03	19	10	07	13	05	06	21	09	05	07	02	02	16	38	18	01	07
7	13	06	07	23	05	06	28	10	13	24	12	05	09	36	00	24	03	03
8		16	01		02	01		03	02		15	01		09	00		01	61
9		10			06			02			09			02			10	
10		10			06			01			02			01			85	

Experiment.	13			14			15			16			17			18		
1	01	00	01	14	01	01	01	81	02	00	05	13	00	23	03	00	01	05
2	47	00	08	12	01	04	02	08	08	00	00	12	00	07	01	01	01	05
3	17	00	05	30	13	28	14	00	00	01	01	06	03	08	01	12	01	05
4	07	02	03	30	13	37	28	01	02	13	01	06	17	01	01	22	01	02
5	03	09	10	02	25	17	18	01	05	21	00	02	16	07	01	23	01	08
6	05	24	20	02	17	10	21	00	02	29	02	03	39	06	01	17	00	05
7	20	10	31	10	05	02	16	00	04	36	01	10	25	03	01	25	01	05
8		10	22		12	01		01	77		01	48		08	91		00	65
9		12			12			01			07			14			06	
10		33			01			07			82			23			88	

Experiment.	19			20			21			22			23			24		
1	00	13	05	01	00	24	01	00	32	01	05	36	10	32	32	00	35	31
2	00	02	07	05	01	14	02	01	15	03	05	15	03	12	08	01	06	11
3	05	01	06	13	01	03	17	00	09	07	02	01	06	05	05	03	08	06
4	12	04	02	21	01	05	13	00	05	15	02	05	13	04	05	07	04	06
5	16	04	02	23	00	05	15	01	07	13	02	05	11	05	04	24	04	08
6	16	01	02	13	01	05	26	01	10	24	02	02	15	03	06	21	03	06
7	51	06	07	24	01	21	26	01	06	37	02	05	42	06	12	44	03	08
8		04	69		01	23		01	16		02	31		06	28		06	24
9		06			06			02			10			05			06	
10		59			88			93			68			22			25	

TABLE II.—Continued

Experiment.	25			26			27			28			29			30		
Position.	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T
1	01	63	23	00	32	10	00	28	17	01	08	04	01	38	28	00	04	08
2	06	08	28	00	05	14	01	07	20	05	06	10	03	11	19	01	04	20
3	11	04	08	00	05	04	01	04	12	23	09	09	05	07	08	01	12	08
4	06	01	13	00	20	03	04	04	06	18	11	09	19	02	07	03	05	09
5	12	01	06	03	08	04	05	03	06	07	06	10	12	04	09	05	06	08
6	18	04	05	05	00	22	16	03	09	16	05	31	18	01	10	13	10	06
7	46	01	08	92	00	42	73	04	13	30	06	16	42	03	13	77	09	13
8		03	09		05	01		06	17		12	11		03	06		14	28
9		06			05			12			18			11			17	
10		09			20			29			19			20			19	
Experiment.	31			32			33			34			35			36		
1	01	97	05	04	40	46	14	32	23	17	13	13	13	15	83	00	16	Not read.
2	09	01	21	04	04	13	05	02	12	07	04	08	06	08	10	01	03	
3	17	00	15	04	04	07	06	05	08	06	04	03	21	07	01	01	04	
4	23	00	13	09	08	03	07	04	08	10	07	04	20	09	01	09	14	
5	26	01	13	11	04	03	07	06	08	11	05	04	16	08	01	20	06	
6	17	00	12	24	04	04	14	07	07	20	07	05	14	05	01	24	07	
7	07	00	17	44	06	07	47	01	10	29	09	16	10	06	02	45	04	
8		00	04		07	17		09	24		07	47		12	01		07	
9		00			06			10			10			19			07	
10		01			17			24			34			11			32	
Experiment.	37			38			39			40			41					
1	04	04	Not read.	01	44	14	05	19	52	00	10	09	01	18	29	Not read.		
2	00	01		06	11	12	11	08	04	01	10	13	00	06	05			
3	01	06		12	05	08	10	04	04	00	12	15	01	04	06			
4	09	08		17	06	06	16	08	04	00	09	18	09	06	11			
5	09	08		14	06	05	19	08	04	00	13	18	22	04	12			
6	32	07		16	04	06	12	10	04	00	10	12	23	06	09			
7	45	06		34	04	08	27	05	06	99	09	09	44	04	14			
8		03			09	41		06	22		09	06		03	14			
9		09			06			11			09			06				
10		48			05			21			09			41				

TABLE III.
Data of others.

Compilation of published data for comparative purposes.						
Schuett (1934) ¹		Volume of Aquaria.		Two aquaria of similar shape were used but the dimensions were not given.		
		7,500 cc.	15,000 cc.			
	Companions.	Meters per Hour.				
	0	200—	150—			
	3	50—	80—			
	7	90+	40+			
	15	110+	90+			
Escobar, Minahan and Shaw (1936) ²			Volume of Aquaria.			
			1,625 cc.	3,250 cc.	4,875 cc.	6,500 cc.
	Fish.	Companions.	Meters per Hour.			
	A	0	83.40	83.44	51.33	118.18
	A	3	17.26	55.47	32.54	58.43
	B	0	103.40	69.43	61.95	100.09
	B	3	39.10	39.65	13.08	50.04
	C	0	81.06	59.58	17.88	108.69
	C	3	24.15	51.84	51.14	17.58
Comparative travel of <i>Carassius</i> from all data.						
	Tank Size.	No. of Alone.	With 3 Companions.	Number of Observation Periods.	Difference.	Values Alone Reduced to Unity. Then Value with +3 =
Escobar	1 ³	92.84	27.58	47	65.26	.30—
Escobar	2 ³	73.95	48.20	47	25.75	.64—
Escobar	3 ³	50.87	27.03	47	23.84	.53+
Escobar	4 ³	109.07	48.77	47	60.30	.45—
Schuett	5	200.00±	50.00±	?	150.00±	.25
Schuett	6	150.00±	80.00±	?	70.00±	.53+
B. & N.	7	76.77	31.55	22	45.22	.41+

¹ Approximate values picked from the published graph.

² Heterotypic associations omitted from this Table. Fish A and B: each value represents the mean of 20 separate 20-minute periods. Fish C: each value represents the mean of 7 separate 20-minute periods. The aquarium used measured 24 x 12 x 24 cm. deep and only the volume of water was varied.

³ These values are weighted A & B—20, C—7. (Range 75 to 34)

TABLE IV.
Comparative travels of *Carassius* in certain experiments.

Rate of Travel M/H.					
Exp. No.	Fish.	Minimum.	Mean.	Maximum.	No. of Periods.
Alone.					
1-6	A	72.96	86.00	101.45	6
15-22	B	49.38	69.84	89.48	8
With 3 Companions.					
7-11	A	17.17	30.48+	42.37	5
12-14	B	14.91	36.66+	50.70	3
Averages.					
Alone		72.96	76.77—	101.45	14
3 Companions		14.91	31.55+	50.70	8

TABLE V.
Mean distribution values for Fish A and B, expressed in percentage.

	A (1-6)			B (15-22)			Average 14		
	V	L	T	V	L	T	V	L	T
Alone.	19	6	56	01	16	15	8	12	33
	14	7	8	02	3	10	7	5	8
	12	4	4	9	2	4	10	2	4
	9	3	4	17	1	3	14	2	4
	10	3	3	18	2	4	15	2	4
	10	2	4	23	2	4	18	2	4
	26	6	6	30	2	7	28	4	7
		8	15		3	53		5	36
		14			7			10	
		47			62			56	
With 3 Companions.	(7-11)			(12-14)			8		
	7	5	12	5	01	2	6	3	8
	16	6	17	21	01	6	18	4	13
	21	10	20	20	4	13	21	8	18
	18	13	16	18	5	16	18	10	16
	14	18	15	10	11	11	12	16	13
	4	15	13	8	14	12	6	15	13
	20	14	06	18	6	12	19	11	8
		9	01		8	28		8	11
		6			11			8	
		4			39			17	

Effect of light on position and speed.

Exp. No.	Watts.	% at Surf.	% at Bott.	% Above Mid.	% Below Mid.	Speed.
35	0	13	10	40	60	95.10
31	10	01	07	39	61	46.49
32	40	04	44	17	82	92.85
33	100	14	47	29	71	86.95
34	200	17	29	35	65	87.48

TABLE VI.

Movements of animals in a shallow circular pan 6 feet in diameter, 2 inches deep.

Fishes.				
No. on Text-fig. 2.	Species.	Clockwise Loops.	Counter-clockwise Loops.	Direction at End of Path.
1	<i>Carassius auratus</i> No. 1	1	1	Counter-clockwise.
2	<i>Carassius auratus</i> No. 2	0	0	Counter-clockwise.
3	<i>Lebistes reticulatus</i> ♀	0	1	Counter-clockwise.
4	<i>Brachydanio rerio</i>	1	1	Counter-clockwise.
5	<i>Villarius catus</i>	0	0	Counter-clockwise.
Total		2	3	

Snails (First Trial).				
				Length of Observation.
Text-fig. 3	<i>Physa</i> No. 1	0	3	10.0 min.
6	<i>Physa</i> No. 2	3	0	13.5
6	<i>Physa</i> No. 3	0	1	16.5
4	<i>Planorbis</i> No. 1	0	0	12.5
6	<i>Vivipara</i> No. 1	1	0	30.0
6	<i>Vivipara</i> No. 2	1	0	30.0

Snails (Second Trial).				
Text-fig. 3	<i>Physa</i> No. 1	0	0	2.5
6	<i>Physa</i> No. 2	0	1	8.5
6	<i>Physa</i> No. 3	0	2	26.0
4	<i>Planorbis</i> No. 1	0	1	22.5

Snails (Third Trial).				
Text-fig. 6	<i>Physa</i> No. 3	1	4	24.0
4	<i>Planorbis</i> No. 1	0	1	

Snail (Fourth Trial).				
Text-fig. 4	<i>Planorbis</i> No. 1	0	0	
TOTAL		6	13	

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